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Effect of lesion size and shape on regeneration of the Red Sea coral *Favia favus*

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ABSTRACT: The present study examined the effect of lesion size and shape on the recovery rates of the scleractinian colonial coral *Favia favus*. Five tissue lesion types, differing in surface area and perimeter, were artificially inflicted on the upper surface of 46 *F. favus* colonies in the shallow reef across from the Marine Biology Laboratory of Eilat (Red Sea). The gradual closure of these lesions was monitored monthly from January to March 1995 by underwater photography. Photographs over time were analyzed with a computerized image analyzer, enabling accurate measurements of the emerging tissue. In this study we present the percent recovery of the various lesion types through time and the ratios between the newly formed tissue and the perimeter length (NFT/P) of each specific lesion. These results show for the first time the significant effect of lesion size and shape on the regeneration capability of a colonial coral. We found that the high recovery rates achieved during the first month are regulated mainly by the perimeter length of the lesion, while during the following months recovery is influenced more by the surface area of the lesion and its surface area/perimeter ratio. The various NFT/P ratios recorded in this study indicate that lesions with a relatively long perimeter probably obtain a higher energetic allocation from the colony, probably due to the larger colony portion associated with their recovery.

KEY WORDS: Lesion shape · Perimeter · Recovery rates · *Favia favus* · Scleractinian corals · Red Sea

INTRODUCTION

Coral tissue is continuously being damaged through the activities of fish, echinoids, asteroids, molluscs, polychaetes and microorganisms (Pearson 1981, Brown & Howard 1985, Hutchings 1986, Cameron et al. 1991). In addition, corals suffer tissue damage from hurricanes (Rogers 1993), sedimentation (Rogers 1990), temperature extremes (Jokiel & Coles 1990), emersion at low tide (Loya 1972), competition (Lang & Chornesky 1990) and human activity (Brown & Howard 1985). Damage to the coral surface is manifested in a variety of lesion shapes and sizes. The bare skeleton then becomes available for settlement by sessile organisms, which pose a potential threat to the survival of the coral colony (Bak & Steward-Van Es 1980). Although lesions can become a permanent feature, some lesions will recover totally through regeneration of the tissue and skeleton (Loya 1976, Bak et al. 1977, Bak & Steward-Van Es 1980, Bak 1983, Meesters et al. 1992, 1994, Meesters & Bak 1993, Van Veghel et al. 1994). Regeneration of an injury starts with the formation of a new tissue layer by the surrounding polyps, and new septa start to emerge in this layer after approximately 2 wk (Meesters et al. 1994). In general, the regeneration of a lesion, expressed in terms of a reduction in lesion size, follows an exponentially decreasing curve (Bak 1983, Meesters et al. 1992, Meesters & Bak 1993).

Although regeneration in colonial corals has attracted many researchers who have speculated on its ecological consequences, most assumptions proposed for colonial corals are based on the regeneration rates of small circular lesions of approximately 1 cm^2 (Bak et al. 1977, Lester & Bak 1985, Meesters et al. 1992, 1994, Meesters & Bak 1993, Van Veghel et al. 1994) and of 5 cm^2 (Bak & Steward-Van Es 1980). An accepted paradigm is that the regeneration of lost tissues is an 'energy-cost' process. This may explain why regenera-

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tion affects colony growth (Bak 1983), reproduction (Rinkevich & Loya 1989, Harrison & Wallace 1990, Van Veghel et al. 1994), resistance to diseases and competitive ability (Bak & Criens 1981). The trade-off in energy allocation between regeneration, reproduction and growth may indicate that corals are capable of controlling and regulating the energy cost of the regeneration process.

The ability to recover lesions is considered to play a fundamental role in the survival of corals. However, the effect of lesion shape on this process has not yet been assessed quantitatively. The objective of the present study was to examine the effect of shape and size of tissue lesions on the recovery rates of the stony colonial coral *Favia favus*, a common species on the shallow reefs of the northern Gulf of Eilat (Red Sea).

MATERIALS AND METHODS

In this study 46 colonies of *Favia favus*, each approximately 45 cm in diameter, were randomly selected in the shallow reef (2 to 3 m) across from the Marine Biology Laboratory of Eilat. Using an air-pick, fueled from a SCUBA tank, 5 different types of tissue lesions were artificially inflicted on the upper part of the colonies, 1 lesion type per colony. The lesions were as follows: (1) single polyp lesions (SP, n = 10; Fig. 1a), (2) elongated lesions composed of 3 polyps in a row (E-3, n = 9; Fig. 1b), (3) square lesions composed of 6 polyps (SQ-6, n = 8; Fig. 1c), (4) elongated lesions composed of 6 polyps in a row (E-6, n = 11; Fig. 1d), and (5) configurations of 3 elongated lesions composed of 6 polyps each, which were inflicted parallel to each other with an interval of 2 undamaged polyps in between (EP, n = 8; Fig. 1e). All lesions were photographed immediately after they were damaged (January 1995) by a Nikonos V camera with 35 mm close-up attachment. Analyzing these slides with an image analyzer (Olympus, CUE-3), we calculated averages (±SD) of the surface areas of the lesions (i.e. projected area), their perimeters and their perimeter/surface area ratios (P/SA; Fig. 2a–c, respectively).

The projected surface areas of the SQ-6, E-6, and each of the 3 lesions in the EP formation were similar (Fig. 2a; 1-way ANOVA, Fisher's PLSD test, $p > 0.05$). These relatively large lesions were followed by surface areas of the E-3 and SP lesions, in decreasing size (Fig. 2a; Fisher's PLSD test, $p < 0.01$). The perimeter lengths of the E-6 types and each of the lesions in the EP formations were similar (Fig. 2b; Fisher's PLSD test, $p > 0.05$.); these were followed by, in decreasing length of perimeter, SQ-6, E-3 and SP lesions (Fig 2b; Fisher's PLSD test, $p < 0.01$). However, there was no significant difference between the perimeter lengths of the SQ-6 (116 ± 8.5 mm; Fig. 2b) and the E-3 lesions (95 ± 7.3 mm). The SP lesions had the highest P/SA ratio (Fisher's PLSD test, $p < 0.01$), with the lowest being for the SQ-6 types (Fig 2c; $p < 0.01$). The E-3, E-6 and each of the EP formation lesions exhibited a similar P/SA ratio (Fig. 2c; $p > 0.05$).

The 5 different lesion types were photographed every month from January to April 1995. Each color slide was analyzed by the image analyzer, enabling accurate measurements of the emerging tissue area over time. The percent recovery of the 5 different lesion types was calculated separately for each of the 3 monthly intervals. In addition, we calculated the percent recovery of the 5 lesion types for the entire study period (90 d). These results were transformed by arcsin$\sqrt{p}$ and tested by ANOVA with repeated measures. The percent recovery of the different lesions obtained during the first month interval was tested additionally by a 1-way ANOVA.

In order to determine the effect of the perimeter length on the regeneration process in *Favia favus*, we calculated the area (in mm^2) of the newly formed tissue (NFT) from the percent recovery data previously recorded for each lesion type for each time interval. These areas of NFT were then divided by the perimeter length of each lesion type, on the basis of the new perimeter at the end of each interval. Using this ratio, we were able to standardize size and shape differences between the 5 lesion types.

RESULTS

The percent recovery achieved by each lesion type during each month interval and throughout the entire study period (relative to lesion size at $t = 0$) is presented in Table 1. The results presented in each column refer only to the changes in lesion size during a given month interval. The highest recovery percentages of all lesion types were achieved during the first month interval followed by a significant decrease during the second and third month intervals (ANOVA with repeated measures, $p = 0.0001$; Table 1).

Throughout the entire study period (90 d) the SP lesions and each of the lesions in the EP formation recovered 59 ± 12.4% and 65.2 ± 15.5% of their initial size, respectively (Table 1). The recovery percentages of these 2 lesion types were followed by those of the E-6, E-3 and SQ-6 lesions, in decreasing order (Table 1). The lowest recovery rates during all 3 time intervals were for the SQ-6 lesions. In addition, the SQ-6 lesions were the only ones to have negative recovery rates during the second and third intervals (Table 1). A

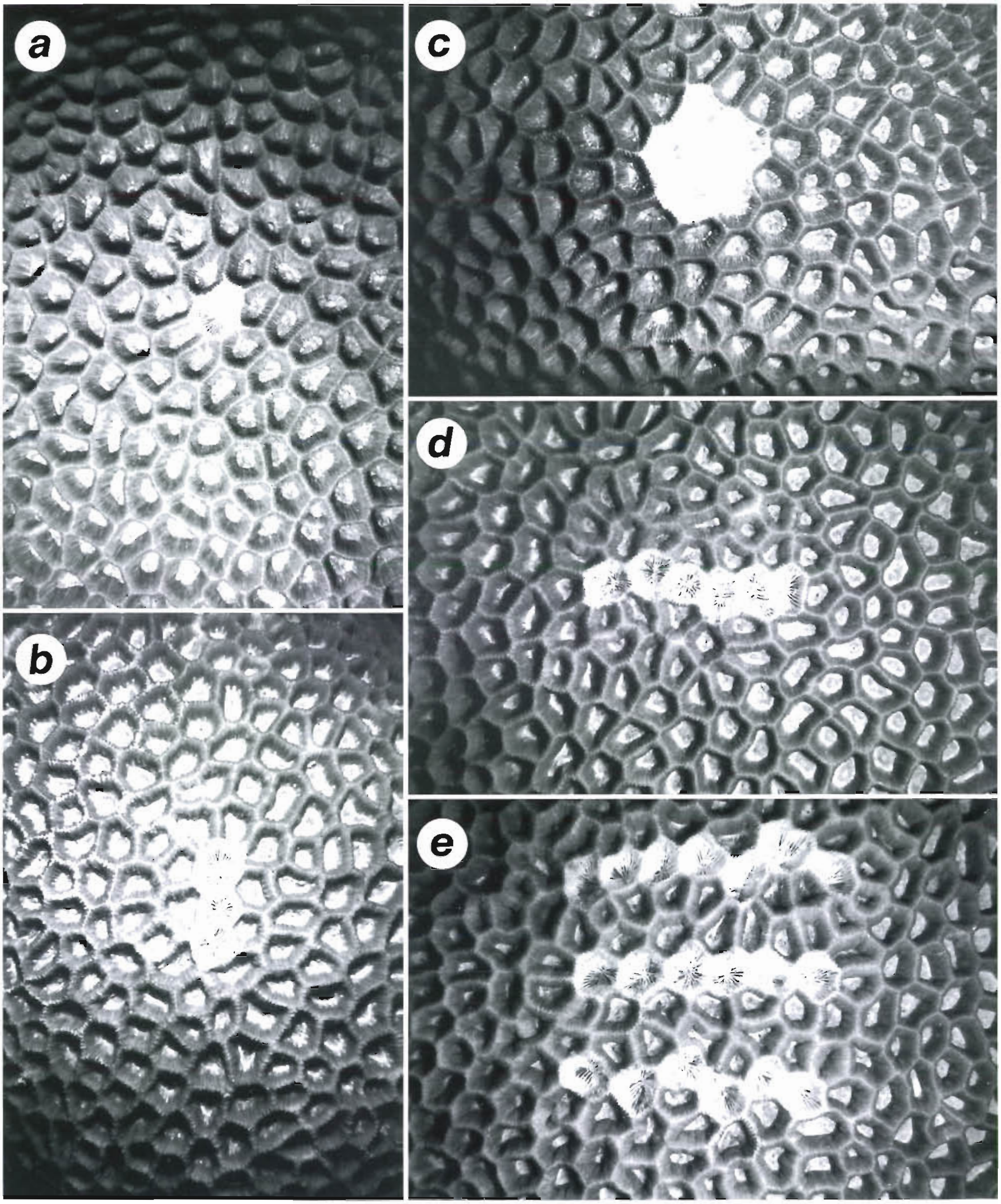

Fig. 1. The different artificial lesions inflicted on the upper surface of *Favia favus* colonies: (a) single polyp lesions (SP); (b) elongated lesions composed of 3 polyps in a row (E-3); (c) square lesions composed of 6 polyps (SQ-6); (d) elongated lesions composed of 6 polyps in a row (E-6); (e) configurations of three 6 polyp elongated lesions parallel to each other with an interval of 2 undamaged polyps in between (EP). All figures at 44% actual size

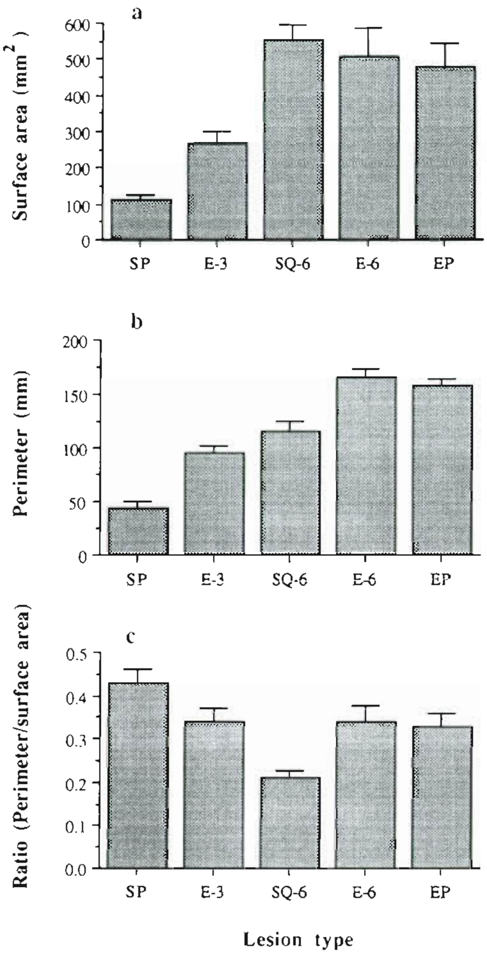

Fig. 2. Characteristics of the 5 different lesion types. (a) Average surface area (+SD); (b) average perimeter length (+SD); (c) average perimeter/surface area (+SD) ratio

survey conducted 12 mo after inflicting the lesions showed that all lesions except SQ-6 had completely healed (data not shown). Furthermore, some of the SQ-6 lesions had doubled their initial size during this period. No significant differences were found between the middle lesions and the external ones in the EP formation (Fig. 1e; 1-way ANOVA, $p > 0.05$).

Table 1. Percent reduction of lesion areas (±SD) during the first interval (30 d), second interval (31–60 d), and third interval (61–90 d) and during the entire study period (0–90 d). SP: single polyp lesions (n = 10); E-3: elongated lesions composed of 3 polyps in a row (n = 9); SQ-6: square lesions composed of 6 polyps (n = 8); E-6: elongated lesions composed of 6 polyps in a row (n = 11); EP: configurations of 3 elongated lesions composed of 6 polyps each, which were inflicted parallel to each other with an interval of 2 unharmed polyps in between (n = 8)

Lesion type	Reduction of lesion area (%) 30 d	31–60 d	61–90 d	0–90 d
SP	43.2 ± 8.1	20.5 ± 5.0	10.3 ± 3.8	59.5 ± 12.4
E-3	24.3 ± 5.1	10.0 ± 3.0	3.6 ± 2.3	34.4 ± 7.9
SQ-6	18.6 ± 3.9	−5.7 ± 2.3	−1.1 ± 1.7	15.9 ± 9.3
E-6	33.6 ± 5.1	16.5 ± 4.7	7.2 ± 3.4	48.6 ± 17.3
EP	48.6 ± 8.2	25.7 ± 5.0	9.0 ± 3.8	65.2 ± 15.5

Table 2. One-way ANOVA of the percent recovery rates (Table 1) attained during the first month. *Significance at 99%. For definitions of lesion type abbreviations see Table 1

Lesion type	Mean Difference	Fisher PLSD
SP vs E-3	11.868	4.887*
SP vs SQ-6	15.615	5.045*
SP vs E-6	5.638	4.647*
SP vs EP	−3.154	4.342
E-3 vs SQ-6	3.747	5.168
E-3 vs E-6	−6.229	4.781*
E-3 vs EP	−15.021	4.485*
SQ-6 vs E-6	−9.976	4.942*
SQ-6 vs EP	−18.768	4.656*
E-6 vs EP	−8.792	4.222*

In the first month interval the elongated lesions of the EP formation attained the highest recovery rates of 48.6 ± 8.2% (Table 1, first interval). The recovery rates of the SP lesions were lower (43.2 ± 8.1%) but did not differ significantly (1-way ANOVA, Fisher's PLSD test, $p > 0.05$; Table 2). However, the percent recovery of both these lesion types were significantly higher than those of E-6, E-3 and SQ-6 (Fisher's PLSD test, $p < 0.01$; Tables 1 & 2, respectively). In addition, we found no significant difference between the E-3 and the SQ-6 lesions (Fisher's PLSD test, $p > 0.05$), which attained the lowest recovery rates during this time interval (Table 1).

The ratios (NFT/P) between the newly formed tissue (in mm²) and the perimeter (in mm) of each of the 5 lesion types for each monthly interval are presented in Fig. 3. The highest NFT/P ratios for all lesions were obtained during the first month and a significant decrease with time was recorded in the following intervals (ANOVA with repeated measures, $p = 0.0001$; Fig. 3).

The NFT/P ratios obtained for the elongated lesions in the EP formation in the first month interval were significantly the highest (Fisher's PLSD test, $p < 0.05$; Fig. 3, Table 3). The second highest NFT/P ratios were for the SP and E-6 lesions, which did not differ significantly between them (Fisher's PLSD test, $p > 0.05$; Fig. 3, Table 3). The NFT/P ratios of the SP and E-6 types were significantly higher than those of the SQ-6 and E-3 lesions (Fisher's PLSD test, $p < 0.05$; Fig. 3, Table 3). However, no significant difference was found between the NFT/P ratios of SQ-6 and E-3 lesions (Fisher's PLSD test, $p > 0.05$).

Table 3. One-way ANOVA of the NFT/P ratios (Fig. 3) attained during the first month. *Significance at 95%. For definitions of lesion type abbreviations see Table 1

Lesion type	Mean Difference	Fisher PLSD
SP vs E-3	0.359	0.183*
SP vs SQ-6	0.192	0.189*
SP vs E-6	-0.001	0.174
SP vs EP	-0.374	0.163*
E-3 vs SQ-6	-0.167	0.194
E-3 vs E-6	-0.360	0.179*
E-3 vs EP	-0.733	0.168*
SQ-6 vs E-6	-0.193	0.185*
SQ-6 vs EP	-0.566	0.175*
E-6 vs EP	-0.372	0.158*

DISCUSSION

The results obtained in this study show that the regeneration process in the colonial coral *Favia favus* is strongly affected by the size and shape of the lesion. We found that in some cases large lesions recovered faster than smaller ones (EP and E-6 vs E-3; Table 1, first interval), and in other cases they recovered at a similar rate (EP vs SP; Table 1, first interval) or more slowly (SP vs SQ-6; Table 1). Bak & Steward-Van Es (1980) found in both *Agaricia agaricites* and *Porites astreoides* that small circular tissue lesions of about 1 cm^2 recovered faster than 5 cm^2 ones. We recorded a similar pattern in *F. favus*, i.e. comparing the recovery rates of the small SP lesions to the E-3, E-6 and SQ-6 lesions (Table 1). However, we found that the recovery rates of these small SP lesions were similar to those of the much larger EP lesions (Figs. 1a, e & 2a, Table 1). The percent recovery rates of the various lesion types revealed that similar sized lesions, such as the SQ-6, E-6 and each of the elongated lesions in the EP formation (Fig 2a), attained different recovery rates despite their size similarity (Table 1).

The only lesions demonstrating negative recovery rates during the second and third time intervals were the SQ-6. The major difference between these and the other lesion types is their relatively low perimeter/surface area ratio (Fig 2c). We noticed that the tentacles of the healthy polyps surrounding each of the elongated (E-3, E-6 and EP; Fig. 1b, d, e) and the SP lesions (Fig. 1a) covered the damaged surface area of these lesions during night time, while the SQ-6 lesions were only partly covered, due to the greater distance between their surrounding polyps and the center of these lesions. Although the surface area of the SQ-6, E-6 and each of the lesions in the EP formation were similar (Fig. 2a), the SQ-6 lesions were more adversely affected by sediment and algae (authors' pers. obs.). We assume that the increase in lesion area recorded in the SQ-6 lesions during the second and third time intervals indicates a possible threshold of wound size and shape for its recovery chances. Sweeper tentacles were not noticed in the lesion areas in any of our night-time observations.

Sousa (1984) proposed that regeneration of benthic organisms is positively related to the ratio between lesion perimeter and its surface area. The high recovery rates of the SP lesions, which obtained the highest P/SA ratios (Fig 2c), versus the low recovery rates of the SQ-6 ones with the lowest P/SA ratios (Fig. 2c), support this presumption. However, in other cases lesions with similar P/SA ratios, such as the E-3, E-6 and each of the EP ones (Fig. 2c), attained different recovery rates (Table 1). Therefore, it seems that the recovery process in colonial corals is more complex and probably regulated by additional factors to lesion surface area or the P/SA ratio of the lesion.

Bak & Steward-Van Es (1980) and Meesters et al. (1994) suggested that regeneration in colonial corals is fueled by a definite and limited energetic resource. In addition, they assumed that the energetic resources required for the recovery of lesions in colonial corals are translocated only from the polyps directly bordering the lesion. In other words, lesions with similar size and shape are therefore expected to achieve similar recovery rates. In our study we found that each of the lesions in the EP formation recovered significantly faster than the E-6 ones despite their similar surface areas and perimeters (Fig. 2, Table 1, first interval). The fact the EP lesions recovered faster than the E-6 ones indicates that energetic resources required for the recovery of the EP lesions can also be trans-

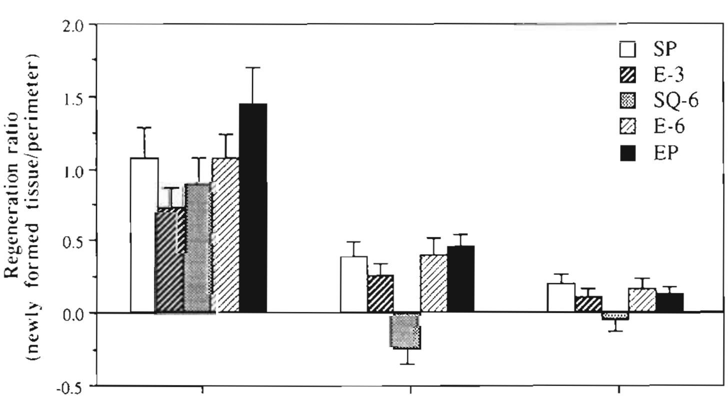

Fig. 3. Average ratios (+SD) between the newly formed tissue (in mm^2) and perimeter length (mm) of each of the 5 lesion types during the first, second and third month intervals

located from polyps that are not directly bordering the lesion.

A comparison of ratios between the newly formed tissue and perimeter length of each lesion (Fig. 3) indicated the importance of perimeter length for tissue regeneration in *Favia favus*. We found that lesions with long perimeters such as the E-6 (165 ± 7.8 mm) had significantly higher NFT/P ratios (see Fig. 3) than lesions with shorter perimeters such as the SQ-6 and E-3 lesions (perimeters = 116 ± 8.5 mm, 95 ± 7.3 mm respectively; Fig. 2b). In other words, lesions with longer perimeters seem to build relatively more new tissue than lesions with shorter perimeters. We propose that the non-significant difference between the NFT/P ratios of the SQ-6 and E-3 lesions during the first month interval (Fig. 3) results from their similar perimeters (116 ± 8.5 mm and 95 ± 7.3 mm, respectively; Fig 2b). The various NFT/P ratios, which standardize the size and shape differences between the lesion types, indicate that different lesions receive different amounts of energy from the colony. The results obtained in this study suggest that long perimeter lesions are provided with greater energetic resources for their regeneration. It is logical to assume that long perimeter lesions in *F. favus* obtain their recovery resources from a large portion of the colony, while short perimeter lesions 'activate' smaller portions of the colony. The high recovery rates and NFT/P ratios demonstrated by the small SP lesions appear to be in contrast to our perimeter length hypothesis. However, we assume that these small, round shaped lesions (Fig. 1a) succeed in reaching optimal regeneration conditions due to the effective protection capacity of the healthy polyp tentacles surrounding them.

The significantly highest NFT/P ratio was recorded in each of the elongated lesions in the EP formation (Fig. 3, first interval). We suggest that these relatively high ratios result from the proximity of these lesions. We further propose that the adjacent lesions (only 2 unharmed polyps between one lesion and the next; Fig. 1e) are 'regarded' by the colony as 1 single lesion with a very long perimeter.

Previous studies showed that regeneration can affect colony growth as well as its reproduction (Bak 1983, Rinkevich & Loya 1989, Harrison & Wallace 1990, Van Veghel & Bak 1994). These findings indicate an energetic trade-off between the polyps of the colony during the regeneration process. The ability of coral colonies to distinguish between different lesions by their perimeter length enables the colony to control its energy flow according to the severity of the lesion.

Regeneration characteristics have been studied for several coral species and are accepted as species specific (Bak et al. 1977, Bak & Steward-Van Es 1980, Bak 1983, Meesters et al. 1992). However, the pattern of declining of these rates over time is ubiquitous in most studied species (Bak 1983, Meesters & Bak 1993). By studying the regeneration of lesions of various shapes in *Favia favus* we demonstrated that the perimeter of the lesion is a key factor in the regeneration rate of lesions in this species. Similar studies on other species may reveal that this regeneration pattern is characteristic for other corals as well.

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